Plant Ecol (2008) 199:201–208
DOI 10.1007/s11258-008-9424-z

# Consequences of nectar robbing for the fitness of a threatened plant species

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Received: 2 November 2007 / Accepted: 14 April 2008 / Published online: 6 May 2008

**Abstract** The effect of nectar robbing on plant fitness is poorly understood and restricted to a few plant species. Furthermore, the available studies generally evaluate the effects of nectar robbing on female fitness, disregarding the male component. Here we measured the effects of the nectar-robbing bumblebees on male (measured as pollen analogue flow distance) and female (measured as seed production) reproductive success in the insect-dependent *Polygala vayredae*, a narrow endemic species from the pre-Pyrenees (Spain). Intense nectar robbing by bumblebees significantly reduced the nectar available to legitimate pollinators in the studied population, and this reduction affected both male and female fitness. Significant differences were observed in fluorescent dye dispersion between robbed and non-robbed flowers within the population. Fluorescent dyes from non-robbed flowers were dispersed to larger distances and over a larger number of flowers when compared with robbed ones. Moreover, significant differences were observed in both fruit set and seed ovule ratios between the two groups, with non-robbed flowers presenting higher reproductive outcomes. However, no effect on seed weight was detected among treatments. The data obtained suggest that in this species, nectar robbing has important indirect and negative effects on plant fecundity, through both male and female functions, due to a modification in the foraging behaviour of legitimate visitors.

**Keywords** Bumblebees · Female fitness · Foraging behaviour · Male fitness · Nectar robber · Reproductive success

## Introduction

Plants that provide floral rewards to attract pollinators frequently attract a wide range of other floral visitors, including nectar robbers. When facing long and narrow or closed corollas, nectar robbers typically make an incision at the base of the tube to reach nectar, without entering into contact with reproductive structures (Inouye 1980). Nectar robbers can directly or indirectly affect a plant and its interactions with legitimate visitors. Several studies have shown direct impacts via removal of floral resources, flower damaging or

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shortening of flower lifespan (e.g., González-Gómez and Valdivia 2005; Navarro 2001; Traveset et al. 1998; Zhang et al. 2007) and indirect impacts which affect legitimate pollinator's foraging behaviour, such as territorial behaviour of nectar robbers (e.g., Roubik 1982) or changes in available nectar (e.g., Irwin and Brody 1998). For example, intense nectar robbing or nectar thieving can indirectly affect legitimate pollinator's behaviours by increasing foraging flight distances (e.g., Maloof 2001; Zimmerman and Cook 1985), reducing the number of visited flowers or inflorescence per patch (e.g., González-Gómez and Valdivia 2005; Hodges 1985; Irwin and Brody 1998) or reducing the time spent per flower (e.g., Thomson and Plowright 1980; Zimmerman and Cook 1985). Consequently, these changes in pollen flow distances and outcrossing rates or alterations in visit efficiency and pollinator fidelity will certainly affect plant reproductive outcome. Although in some cases nectar robbers may act as direct mutualists (e.g., Higashi et al. 1988; Navarro 2000; Navarro et al. 1993) or even present a neutral effect in plant reproduction (e.g., Arizmendi et al. 1996; Stout et al. 2000), most of the accumulated evidence indicates direct or indirect negative effects on plant fitness (e.g., Irwin and Brody 1999; Irwin et al. 2001; Roubik 1982; Traveset et al. 1998; Zhang et al. 2007). Thus, it is clear that the effect of nectar robbing on plant reproductive success results from a complex and variable array of positive, neutral or negative interactions rather than a simplistic single side-effect scenario (Irwin et al. 2001; Maloof and Inouye 2000).

From the plant perspective, most studies on nectar robbing have only considered the effects of nectar robbers on the maternal plant function (for a review see Irwin et al. 2001; Maloof and Inouye 2000). However, in hermaphroditic plants, reproductive success is the sum of gains obtained through both male and female functions. Because seed production is often pollen and/or resources limited, pollinator visitation behaviour may more strongly affect seeds sired than seeds produced (e.g., Irwin and Brody 2000; Young and Stanton 1990; references therein). Therefore, to accurately assess the effects of nectar robbing on plant fitness, both male and female functions should be considered. Although the impact of nectar robbing or nectar thieving on plant fecundity has already been assessed in various tropical and temperate plant species, only a few studies have examined both male and female reproductive outcomes in relation to nectar larceny (Fritz and Morse 1981; Irwin and Brody 1999; Morris 1996; Wyatt 1980; Zhang et al. 2007).

*Polygala vayredae* Costa (Polygalaceae) is a narrow endemic species from the oriental pre-Pyrenees (Spain), with long closed corolla tubes and nectar rewards located at the base of the floral tubes. Despite the fact that flowers of *P. vayredae* receive visits from more than 24 floral visitors, this species frequently suffers pollen limitation due to pollinator scarcity, with just two species of long-tongued bees (*Anthophora* sp. and the bumblebee *Bombus pascuorum*) and two pollinivorous species (*Eucera longicornis* and *Halictus* sp.) behaving as legitimate pollinators. Only these species are able to move the keel downwards and enter in contact with the reproductive structures when probing for nectar or collecting pollen. The remaining species act as nectar robbers, secondary nectar robbers or nectar thieves (sensu Inouye 1980). A set of six different species of short-tongued bumblebees (of which *B. terrestris* was most frequent) were active nectar robbers, accounting for 64.2% of the total visits during 2005–2007 (Castro 2007). In fact, the frequency of nectar robbing assessed during this period was always above 80% (Castro et al. 2008a). Furthermore, due to the closed structure of the flower, nectar robbers do not enter in contact with the reproductive structures and thus never accidentally pollinate the plant. Also, no significant floral damages induced by nectar robbers have been observed (Castro et al. 2008b).

The knowledge of these intense (robbers) and crucial (pollinators) plant–animal interactions occurring in *P. vayredae* led us to consider whether nectar robbing would indirectly affect the reproductive outcome of this species. To address this question, the effect of nectar robbing on male and female fitness was experimentally measured, through pollen analogues flow distance and seed production, respectively. The effect of nectar robbing on available nectar was also estimated. This study constitutes the first report on the effects of nectar robbing on the *Polygala* genus and contributes with valuable information needed to understand the striking consequences of nectar robbing on plant fitness and plant–animal interactions.

## Material and methods

### Plant and study area

*Polygala vayredae* is a narrow endemic species restricted to an area of approximately 12 km$^2$ in Alta

Garrotxa, Girona (Catalunya, Spain), where it occurs in a few dense populations. According to IUCN categories, a preliminary endangered status has been given to this plant (vulnerable; VV.AA. 2000). This species is a small shrublet, annually sending up shoots from a rootstock and forming dense clusters of several individuals. One-year-old ramets produce small axilar inflorescences of one to three flowers in early spring (April–May), with each flower having a bilocular ovary with one ovule per locule. The large, self-incompatible papilionate flowers possess a long corolla tube formed by the two lateral petals (14.5 ± 0.78 mm long; for illustrations see Castro et al. 2008b). Nectar is produced at the base of the corolla (daily nectar production: 1.9 ± 0.86 μl with 16.0 ± 6.23% of sugar), and flowers are able to re-synthesize after several removals (Castro et al. 2008b). Furthermore, flowers possess a mechanism of secondary pollen presentation, where the pollen is presented to the pollinators in a specialized region of the stigma (the pollen presenter; Castro et al. 2008c). Fruiting occurs in late spring (May–June) with the production of a dehiscent capsule (10.0 ± 1.04 mm long and 8.8 ± 0.79 mm wide) containing two seeds (4.7 ± 0.24 mm long, each weighting 9.1 ± 1.62 mg, dry weight) (Castro 2007).

The present study was carried out during the spring of 2007 in the population of Colldecarrera at the natural protected area of Alta Garrotxa (UTM DG57). This population occurs at 630 m altitude, in mesophytic and xeric meadows (*Mesobromion*) with *Pinus sylvestris* and *Buxus sempervirens*, under the *Quercetum pubescentis* domain. In this population, *P. vayredae* is the dominant species, forming dense carpets of hardly distinguishable individuals. Fruit set in previous years varied between 47.6% in 2005 and 21.0% in 2006 (Castro 2007; Castro et al. 2008b). This population was selected due to its accessibility and pollinator availability.

### Nectar availability

The amount of available nectar in robbed and non-robbed flowers was assessed daily during the first hours of the morning (usually between 0800 and 1000, GMT) over eight consecutive days in 115 randomly selected flowers along the population. Robbed flowers were easily recognized, due to the visible and repeated incisions made in the corolla by robbers. Nectar production was measured with capillary micropipettes and sugar concentration was determined (in w/w%) using a portable refractometer. The amount of sugar produced by each flower was calculated following Prys-Jones and Corbet (1987).

### Effects of nectar robbing on pollen flow

To evaluate the effect of nectar robbing on male fitness (pollen dispersion), fluorescent powdered dyes (Radiant Colour, Richmond, CA, USA) were used as pollen analogues (Waser and Price 1982). It has been previously observed that dye transfer closely resembles pollen transfer when bumblebees are the pollen vector (e.g., Adler and Irwin 2006; Rademaker et al. 1997; Waser 1988), despite the different dispersal properties of the dye and pollen grains (Thomson et al. 1986). A 0.25 $m^2$ cluster with flower buds was protected with a mosquito net to prevent nectar robbing. When flowers opened, the mosquito net was removed and two sets of flowers were prepared: (1) non-robbed flowers—fluorescent dye was applied on the pollen presenter of 30 newly open flowers protected at the base of the corolla using transparent tape, to prevent nectar robbing and 2) robbed flowers—fluorescent dye of a different colour was applied on the pollen presenter of 30 newly open flowers, daily subjected to nectar robbing. Nectar robbing was performed by cutting a hole at the base of the corolla and removing the available nectar daily with micro-capillary tubes. Three replicates, separated by distances of over 100 m, were set up within the population at the same time. Furthermore, in the intermediate replica different coloured dyes were used to avoid erroneous results. After 8 days, 45–50 flower samples were collected at several distances from each cluster source (1, 2, 3, 4, 5, 10, 25–50, 50–100 m) along two opposite linear transects starting in each cluster. The flowers were preserved at −4°C. In the laboratory, flowers were examined under UV light using a stereo binocular microscope. The presence/absence of each dye powder deposited on the stigma was recorded for each distance.

### Effects of nectar robbing on fruit production and seed weight

To evaluate the effects of nectar robbing on female fitness (fruit and seed production), 500 flower buds were randomly selected along the population during the flowering period and the following treatments were applied: (1) flower buds were protected from nectar robbing, (2) flower buds were subjected to daily nectar robbing after anthesis (according to the procedure described above) and (3) unmanipulated flowers were left for open visitation as a control. Flowers were open-pollinated and fruit and seed production were recorded when mature. Fruit set (i.e., proportion of flowers that developed fruits) and seed ovule ratio (i.e., proportion of ovules that developed seeds) were calculated. Seeds were collected to determine seed weight. In the laboratory, seeds were dehydrated under natural conditions, maintained in a vacuum desiccator with silica gel for 24 h and weighed in an analytical balance (0.01 mg precision).

### Statistical analysis

The differences in nectar volume and sugar amount between robbed and non-robbed flowers were analysed with a Mann–Whitney rank sum test, while nectar concentration was analysed with a $t$ test. The proportions of robbed and non-robbed flowers without nectar rewards were analysed with a $z$ test.

The proportions of flowers with fluorescent dye for each distance (categorical data) were adjusted to a binomial distribution and analysed with generalized linear model with a logit link function. A type 3 likelihood-ratio test was computed. The proportions of flowers receiving fluorescent dye from robbed and non-robbed flowers were analysed with a $z$ test.

The effects of nectar robbing on fruit set and seed ovule ratio were evaluated with a $\chi^2$ test; comparison of more than two proportions and multiple comparison tests for proportions were made in accordance with Zar (1984). Differences among treatments in seed weight were analysed with a one-way ANOVA. The general linear model procedure was followed due to unbalanced data.

## Results

### Nectar availability

Robbed and non-robbed flowers of *P. vayredae* presented different nectar rewards (Table 1). The nectar volume encountered in non-robbed flowers was significantly higher than the one found in robbed flowers ($T = 1593.5$, $P = 0.001$). Furthermore, although no significant differences were observed in the mean nectar concentration ($t = 0.24$ $P = 0.812$), the mean amount of sugar (i.e., energy) collected in non-robbed flowers was significantly higher ($T = 1552.0$, $P = 0.004$). Moreover, intense nectar robbery seemed to significantly decrease the ability of the flower to re-synthesize nectar ($z = 2.18$, $P = 0.029$), as a high proportion of robbed flowers stopped nectar production, losing one important pollinator attractive feature (Table 1).

### Effects of nectar robbing on pollen flow

Both robbed and non-robbed flowers of *P. vayredae* were able to disperse pollen. However, a significantly higher pollen flow ($z = 3.14$; $P = 0.002$) was observed in non-robbed flowers (4.1%) in comparison with robbed ones (1.9%). In both cases, pollen flow was found to be higher in the first few metres, and was drastically reduced as the distance to the focal clusters increased ($\chi^2 = 68.11$, $P < 0.001$ and $\chi^2 = 42.49$, $P < 0.001$ for non-robbed and robbed flowers, respectively; Fig. 1).

**Table 1** Nectar available in robbed and non-robbed flowers of *Polygala vayredae* in Colldecarrera population during the spring of 2007

| Treatment | $n$ | Volume (µl) | Nectar concentration (%) | Sugar amount (mg) | Proportion of rewardless flowers (%) |
|---|---|---|---|---|---|
| Robbed flowers | 95 | 0.34 ± 0.772 | 70.2 ± 19.99 | 0.15 ± 0.266 | 44.2 |
| Non-robbed flowers | 20 | 0.67 ± 0.597 | 71.5 ± 23.41 | 0.33 ± 0.322 | 15.0 |
| Comparison test | | $T = 1593.5$*** | $t = 0.24$ n.s. | $T = 1552.0$** | $z = 2.18$* |

Volume, nectar concentration and sugar amount are given as mean and standard deviation of the mean; for the calculation of mean nectar concentration, rewardless flowers were excluded; *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; n.s., not significant

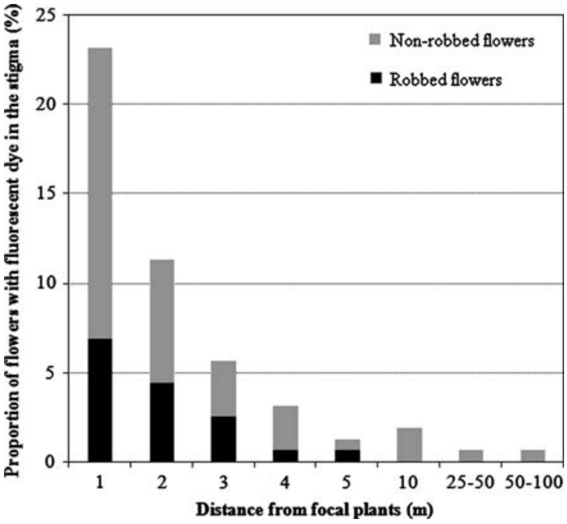

**Fig. 1** Fluorescent dye dispersion among robbed (dark grey) and non-robbed (light grey) flowers of *Polygala vayredae*. Proportions of flowers with fluorescent dye in the stigma represented as a function of the distance to the cluster of focal plants

## Effects of nectar robbing on fruit production and seed weight

Fruit set and seed ovule ratio were significantly affected by nectar robbing ($\chi^2 = 6.94, P < 0.05$ and $\chi^2 = 23.39$, $P < 0.001$, respectively; Table 2). Non-robbed flowers and control flowers produced significantly more fruits and seeds than robbed flowers ($P < 0.05$). No significant differences in seed weight were observed among treatments ($F = 1.83, P = 0.163$).

## Discussion

Nectar robbing is an ecological interaction widely distributed in temperate and tropical regions, with bumblebees being common nectar robbers of many flower species (Inouye 1983; Irwin and Brody 2000; Morris 1996; Navarro 2000). As nectar robbers can affect interactions between a plant and its legitimate pollinators (e.g., Irwin et al. 2001; Maloof 2001), they cannot be disregarded when studying the fitness of flowering plants. However, due to the scarcity of available information, the actual role of nectar robbing on plant–pollinator interactions, and its impacts on reproductive outcomes are largely unknown (see review in Irwin et al. 2001; Maloof and Inouye 2000). The present study provides the first report of the consequences of nectar robbing for reproductive success within the *Polygala* genus.

Nectar robbing can deeply influence the patterns of nectar availability, and this change may affect flower attractiveness and floral visitor's behaviour (e.g., González-Gómez and Valdivia 2005; Irwin and Brody 1998; Irwin et al. 2001; Maloof 2001; Zimmerman and Cook 1985). Previous observations have indicated that nectar robbers were steady components of *P. vayredae* flower–visitor interactions (Castro 2007; Castro et al. 2008a). In the present study we show that they affected nectar availability in the studied population during the spring of 2007. When visiting robbed flowers, floral visitors obtained less nectar rewards and consequently, less energy. Furthermore, floral visitors frequently encountered rewardless flowers (39%). These observations suggest variable and unpredictable nectar availability in the population because of nectar robbing. Reductions in nectar availability, or changes in nectar production patterns as a result of exploitation by nectar robbers, have been observed in several other species (e.g., *Mertensia paniculata* L., Morris 1996; *Macleania bullata* Yeo, Navarro 1999; *Moussonia deppeana* Klotzsch ex Hanst., Ornelas

**Table 2** Fruit set, seed ovule ratio and seed weight in open-pollinated flowers of *Polygala vayredae* subjected and not subjected to nectar robbing

| Treatment | *n* | Fruit set (%) | Seed ovule ratio (%) | Seed weight (mg) |
|---|---|---|---|---|
| Robbed flowers | 200 | $15.5^a$ | $12.3^a$ | 8.23 ± 1.425 |
| Non-robbed flowers | 200 | $25.0^b$ | $18.8^b$ | 7.86 ± 1.099 |
| Control | 100 | $26.0^b$ | $17.5^b$ | 8.27 ± 1.396 |
| Comparison test | | $\chi^2 = 6.94$* | $\chi^2 = 23.39$** | $F = 1.83$ n.s. |

Fruit set (proportion of flowers that developed fruits) and seed ovule ratios (proportion of ovules that developed seeds) are given as percentages, and seed weight is given as mean and standard deviation of the mean; data were collected in Colldecarrera population during 2007; different letters reveal significant differences; *$P < 0.05$, **$P < 0.001$; n.s., not significant et al. 2007; *Puya coerulea* Miers, González-Gómez and Valdivia 2005). Results of this include subsequent impacts on the total nectar produced per flower (Ornelas et al. 2007; Navarro 1999) and changes in the pollinator's visitation patterns (González-Gómez and Valdivia 2005; Morris 1996). Furthermore, in several species, lack of nectar may result from damages inflicted by the nectar robber on the flower and nectar gland (e.g., González-Gómez and Valdivia 2005; Traveset et al. 1998). This was not the case for *P. vayredae* where, despite some damages caused to the corolla, the reduction in available nectar was the result of successive nectar extractions, with no harm inflicted on the nectar gland (Castro et al. 2008b).

In *P. vayredae*, pollen dispersal appears to be negatively affected by nectar robbing, as high levels of nectar robbing reduced the dispersal distance of fluorescent dye within the studied population. Furthermore, as pollen analogues from robbed flowers were not found at far distances from the cluster source, it seems that the lack/low resources of these flowers lead pollinators to change their behaviour and leave the population. On the other hand, pollen from non-robbed flowers was dispersed far away within the population, despite a drastic decrease in the number of visited flowers was observed as the distance from the cluster source increased. Although the consequences of nectar larceny on male function have been examined in few plant species, different effects have been observed. For example, in *Mertensia paniculata*, nectar-robbing bumblebees had a positive effect on pollen removal in young flowers but no impact on the final male fitness of the flower (Morris 1996), while in *Asclepias syriaca* L., no effects of nectar-thieving ants on pollinia removal were observed (Fritz and Morse 1981). On the other hand, in *Ipomopsis aggregata* (Pursh) V.E.Grant, nectar-robbing bumblebees considerably decreased pollen donation, negatively affecting the male function (Irwin and Brody 1999). To some extent, nectar robbing has been regarded as a positive interaction when the change in pollinator's behaviour results in an increase in the distance of between plant flights (improving pollen dispersal and thus gene flow; e.g., Maloof 2001; Zimmerman and Cook 1985) or in a decrease in the visitation rate within inflorescences or plants (reducing geitonogamous pollination; e.g., Hodges 1985; Klinkhamer and de Jong 1993). However, in other cases legitimate pollinators may switch to different plant species or even leave the population (e.g., Roubik 1978, 1982. The behaviour of *Bombus pascuorum* (the main pollinator in the studied population) seems in accordance with the results obtained in the pollen flow experiment. This bumblebee is usually observed exploiting a high number of flowers within a patch when nectar availability is high (as in the blossom beginning) and a lower number if the quantity of nectar is more variable due to high nectar robbing (as in the blossom peak). However, in both cases, when *B. pascuorum* leaves the flower clusters, it always flies away several metres, sometimes even out of sight, before starting new flower exploitations (S. Castro, personal observations). Thus, pollinators fly further within the population after visiting non-robbed flowers in search of more food rewards and were more likely to leave the population after visiting several rewardless flowers subjected to high nectar robbing. This is only partially in accordance with the foraging theory. While it seems that the pollinator leaves the cluster (or even the population) when the rate of energy intake is lower than the potential energy intake available in the habitat (Charnov 1976), an inverse relationship between nectar rewards and interplant pollinator flight distance (Pyke 1978) was not observed. However, this theory is based on the assumption that pollinators had no previous knowledge of flower's reward status. The main pollinators of *P. vayredae* appeared to selectively visit non-robbed flowers, which may indicate a prior recognition of the available rewards or scent marks left by previous floral visitors (Goulson et al. 1998). If this is the case, predictions about pollinator's foraging behaviour could be significantly altered. Additionally, special care must be taken when interpreting the drastic reduction in fluorescent dye dispersal with increasing distance from the cluster source. This result could be detrimentally affected by the increase in the sampling area rather than reflect only the foraging behaviour of the main pollinators. Further studies monitoring different robbery frequencies, available rewards, and pollinator's visitation rates and behaviour are needed to better understand these complex plant–animal interactions.

Regarding female fitness, nectar robbing significantly decreased the number of fruits and seeds produced. In a meta-analysis study, integrating available work on nectar robbing effects, Irwin et al. (2001) observed that in general floral larceny had weak but negative effects on female reproductive success. Furthermore, the authors observed that the type of larcenist and pollinators had significant impacts on the resulting fitness. For insect-pollinated plants, floral larceny by other insects had a weak positive effect. However, this result was probably influenced by the fact that there are several mutualistic plant–robber interactions where the insect accidentally pollinates the flower (e.g., Higashi et al. 1988; Navarro 2000; Navarro et al. 1993). In *P. vayredae*, as the corolla is a closed structure, nectar robbers were never involved in pollination, exerting an indirect negative effect on the realized female fitness. Similar observations were obtained, for example, in *Ipomopsis aggregata* (Irwin and Brody 1998), *Vitex negundo* L. (Reddy et al. 1992), *Quassia amara* L. (Roubik et al. 1985) and *Duranta repens* L. (L. Navarro and R. Medel, unpublished data). On the other hand, seed weight was not affected by nectar robbing. This agrees with previous observations of nectar production patterns, where intense nectar robbing also decreased the total amount of nectar produced per flower (S. Castro, unpublished data). From these results, it seems that in *P. vayredae*, nectar robbing did not affect seed weight through energetic investment in nectar re-synthesis, contrarily to what has been observed in other species (Pyke 1991; Southwick 1984).

Taken together, the results obtained in the present study suggest an indirect negative effect of the nectar robbing on plant reproductive outcomes, through a decrease in available nectar and consequent changes in the visitation behaviour of legitimate pollinators. When avoiding robbed flowers or leaving the population, the pollinators reduced pollen flow and dispersal distances (male function), as well as fruit and seed production (realized female fitness). Considering the lack of studies on the cumulative effects of robbing on both male and female functions, the importance of nectar robbers to plant ecology and evolution may have been underestimated in the past and should be further considered in future studies.

**Acknowledgements** The authors thank the *Departamento de Medi Ambient* of *Generalitat de Cataluña* and the *Consorsi d'Alta Garrotxa* for allowing this research and the *Parc Natural de la Zona Volcànica de la Garrotxa* for all the assistance. The authors also thank João Loureiro and colleagues on the project CYTED 2003-XII-6 for critical reading of the manuscript. The Portuguese Foundation for Science and Technology financed the work of Sílvia Castro (FCT/BD/10901/2002). The work was also partially financed under grants to Luis Navarro, PGIDT04PXIC31003PN from the Xunta de Galicia and CGL2006-13847-CO2-02 from the Spanish DGICYT.

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